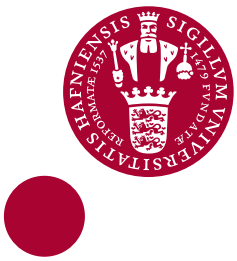

# Resource tracking within and across continents in long-distance bird migrants

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# Resource tracking within and across continents in long-distance bird migrants

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**Migratory birds track seasonal resources across and between continents. We propose a general strategy of tracking the broad seasonal abundance of resources throughout the annual cycle in the longest-distance migrating land birds as an alternative to tracking a certain climatic niche or shorter-term resource surplus occurring, for example, during spring foliation. Whether and how this is possible for complex annual spatiotemporal schedules is not known. New tracking technology enables unprecedented spatial and temporal mapping of long-distance movement of birds. We show that three Palearctic-African species track vegetation greenness throughout their annual cycle, adjusting the timing and direction of migratory movements with seasonal changes in resource availability over Europe and Africa. Common cuckoos maximize the vegetation greenness, whereas red-backed shrikes and thrush nightingales track seasonal surplus in greenness. Our results demonstrate that the longest-distance migrants move between consecutive staging areas even within the wintering region in Africa to match seasonal variation in regional climate. End-of-century climate projections indicate that optimizing greenness would be possible but that vegetation surplus might be more difficult to track in the future.**

## INTRODUCTION

Recently, there have been increasing efforts to understand the association between animal movement and the environment. Studies have linked distributions and movements of diverse marine organisms to sea surface temperature and net primary productivity (NPP) (*1*, *2*), whereas elephants track precipitation-driven vegetation dynamics (*3*) and other ungulates wander to optimize the nutritional content of the grasses they eat (*4*, *5*). Migrating birds also track vegetation dynamics, the so-called green wave surfing; that is, the birds move northward, timed with the seasonally progressing green-up of vegetation (*6*–*8*).

The ability to fly makes birds one of the most mobile terrestrial animals (*9*, *10*). Long-distance migratory birds commonly explore distantly separated regions between breeding and wintering grounds. They often do so by traveling several thousand kilometers and crossing large inhospitable regions to find areas where environmental conditions can sustain survival (*11*, *12*). In this way, seasonal migration solves the problem of exploiting seasonal resources across the globe (*11*).

Remote sensing data, such as the satellite-based greenness index NDVI (Normalized Difference Vegetation Index), are increasingly used to infer ecological processes related to movement. Using NDVI, it has been suggested that geese migrating to breeding grounds, at least in some cases, "surf the green wave" of sprouting high-quality grass vegetation (*6*, *8*, *13*, *14*). Likewise, regional winter movements of Montagu's harriers (*Circus pygargus*) have been correlated with decreasing vegetation greenness (*15*), and bobolinks (*Dolichonyx oryzivorus*) have been shown to leave grasslands used for stopovers when vegetation conditions deteriorate (*16*). Moving from breeding grounds in the Northern Hemisphere to wintering grounds in the Southern Hemisphere obviously enables the exploitation of surplus seasonal resources with a clear dynamic link between breeding and wintering resources (*17*–*20*). However, the study of the underlying migration pattern drivers throughout more complex annual spatiotemporal schedules has been hampered by the lack of data on the movements of individual birds throughout the year, especially within their tropical wintering area.

Moreau (*21*) suggested that, in Africa, many migrants follow a strategy of itinerancy, staying in areas only while they are most suitable after seasonal rains. In this way, areas south of the equator become suitable during the austral summer, enabling only the longest-distance migrants, such as thrush nightingales (*Luscinia luscinia*) and red-backed shrikes (*Lanius collurio*), to exploit these areas. Inferred from observations of seasonal occurrence, these itinerant schedules have been suggested for thrush nightingales and red-backed shrikes but not for common cuckoos (*Cuculus canorus*) (*22*–*24*).

However, the hypothesized link between movements and seasonal regional resources throughout the annual cycle has never been properly established, and the precise timing of annual individual schedules relative to seasonally induced local dynamics in habitats, food resources, and climate remains restricted to parts of the annual cycle in long-distance migrants (*6*–*8*, *13*, *15*, *16*, *25*). In order to establish potential links between resources and annual bird movements, we have combined the results of high–temporal resolution tracking of individual birds with monitoring variation in local ecological conditions across the seasonally changing globe. On the basis of these links, we evaluate the potential consequences of end-of-century climate projections.

Overall, birds exploiting seasonal environments need to properly schedule annual events to maximize fitness (*26*). The optimal timing

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of events, such as breeding and molting as well as migration, depends on the availability of seasonally changing resources within the annual cycle (*27*). Resource availability is likely to be most important during breeding; thus, timing of breeding in relation to resource availability will be more important than stopover timing. Arrival well before the peak in insect prey abundance is common in migrants (*28*, *29*), and it may be impossible to consistently maximize local resources throughout the annual cycle.

Food availability is likely to be the most important resource throughout the annual cycle (*30*, *31*), presumably explaining migration to breed at higher latitudes (*32*) and stopover timing during spring migration (*33*). Arzel *et al.* (*28*) found that breeding coincides with a peak in invertebrate food abundance in migratory ducks but failed to find support for the hypothesis that they would gain a general increase in food abundance by flying north during spring. Other studies have assumed that migrants were either tracking a climatic niche (*34*) or staying only during a short period with optimal resource availability, mainly limited to the migratory part of the annual cycle (*15*, *16*).

In general, availability of resources such as food is very difficult to estimate, particularly across habitats and climate zones. We focus on general vegetation measures to estimate food availability on the basis of the well-established principle that food availability is ultimately related to plant productivity (*35*).

Staying in the greenest vegetation potentially leads to generally high food availability such as that resulting from breeding in the Northern Hemisphere during summer and spending the nonbreeding season in the Southern Hemisphere (*36*). The accelerating vegetation growth during spring green-up provides another potentially high food availability, also known as surfing the green wave (*6*, *13*), although, for insectivores, the food peak is generally delayed. Avoiding decreasing vegetation conditions could also drive movements (*15*, *16*).

Given the complexities of niche tracking through different climatic zones and the variable demands during breeding and wintering periods, we propose that, instead of following green vegetation conditions or a constant climatic niche, some migrants might use an alternative strategy of more broadly following pulses of resources, that is, high relative availability of local seasonal resources (surplus greenness; see later discussion). Food availability depends not only on productivity but also on the density of consumers sharing the food resource. Resident populations are thought to be limited by food availability during the season when food availability is at its lowest, whereas clutch size is determined by per-capita food availability during the season when food availability is at its highest (*37*), and seasonality (the difference between minimum and maximum level of resources) has been linked to clutch size (*38*, *39*). Therefore, migrants may potentially be able to exploit excess or surplus resources in seasonal environments where the density of residents is regulated by the productivity in the season where productivity is lowest (*40*, *41*).

We hypothesize that the migrants' spatiotemporal schedules could maximize greenness, surplus greenness, or change in greenness. We assume that prolonged migration to new staging sites would generally occur based on the expected conditions at the new site rather than on the actual conditions (unknown to the birds) that, at the time of movement, must be considered. Proximate cues presumably only affect local movements [for example, as reported for within-winter movements in a short-distance migrant songbird (*42*)] because migrants are expected to rely on their innate program to guide them over long distances (*43*), with this program presumably being adapted to longer-term averages of climate/resource availability. Songbird migrants have been shown to regionally use the same stopover areas for years, irrespective of local conditions (*44*). Thus, we focus our analyses on average vegetation conditions over a decade to reflect the expected conditions for a migrant.

Newly developed satellite tracking and light level–based geolocation technology now enables us to follow individual, long-distance migratory birds throughout their annual cycles, which permits more direct inferences about the drivers of long-distance migration and regional movements of individuals (*45*). Using this technology, we followed common cuckoos ($n$ = 8) (*46*), red-backed shrikes ($n$ = 18) (*44*, *47*), and thrush nightingales ($n$ = 12) (*44*), between the Palearctic and southern Africa. The migration routes of these three insectivorous species include large parts of Europe and Africa.

We used a satellite-based greenness index, NDVI, to study spatiotemporal dynamics in food availability caused by seasonal variation in sun radiation and rainfall. Local greenness at an intercontinental scale was measured by averaging the observed NDVI between 2000 and 2010 at a biweekly temporal resolution in 2° latitude × 2° longitude squares (absolute greenness; fig. S1). Local biweekly NDVI relative to the annual average (local surplus in greenness; surplus NDVI) was used as a proxy for ephemeral peaks in food resources. Furthermore, we calculated the change in greenness from the previous biweekly period (change NDVI). Migratory animals need to fit their annual schedule to the seasonally available resources (*48*). We built a simple, coarse-scale simulation framework to investigate whether the observed schedules were optimal with regard to greenness, surplus greenness, or change in greenness compared to an assumption of no optimization (*49*). The level at which birds select their habitat is not reflected in the available climate data, and favorable conditions could easily exist locally. However, these local conditions could potentially not be driving long-term spatiotemporal schedules. Combined with the large-scale simulation and the similarity in schedules within species, our relatively small sample sizes are likely to reflect each species' overall resource optimization at the near-global level.

The amount of future suitable nonbreeding habitat is expected to decrease for some sub-Saharan migrants and to increase for others (*50*). Regardless, suitable areas based on climate change projections will generally be further away from the breeding grounds for trans-Saharan migrants (*51*). Projections of future climate imply that the spatiotemporal distribution of resources will change, potentially leading to a future mismatch between seasonal resources and birds' presence (*52*). We investigated this potential future mismatch by comparing observed migration schedules with end-of-century projections of seasonal vegetation greenness and local surplus of greenness (that is, greenness and surplus greenness, using the decade-wide climatology).

## RESULTS

Migration patterns among individuals differ considerably among the three species examined. Our data reveal that individuals of the three species had many consecutive stopovers within Africa. The movement among stopovers results from birds being able to narrowly follow the complex seasonal vegetation changes occurring within sub-Saharan Africa. Population patterns consistently matched the high levels of food supply throughout the birds' migration routes ($P < 0.001$ for all species, sign test by biweekly period for greenness above average; Figs. 1, 2, and 3A), with considerable fluctuation within and among

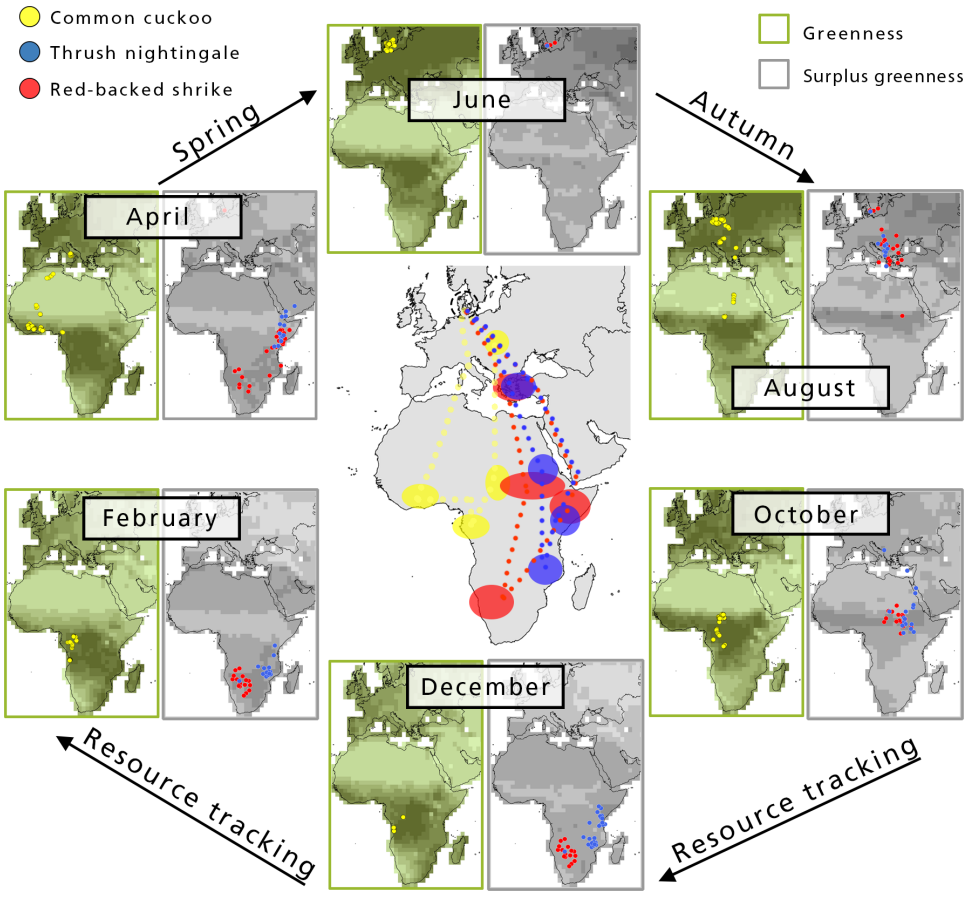


**Fig. 1. Spatiotemporal distribution of individuals of three transhemispheric migrant bird species in relation to seasonal changes of absolute and local surplus vegetation greenness (NDVI) during the annual cycle.** The map in the center shows the annual migration with general stopover areas of the common cuckoo, red-backed shrike, and thrush nightingale indicated in yellow, red, and blue lines, respectively. Maps compare patterns of greenness (maps on the left side; dark green, high average NDVI) and local surplus greenness (maps on the right side; dark gray, high average surplus NDVI) every 2 months from the breeding season (June) through changing species-specific nonbreeding stopover locations. Cuckoos ($n$ = 8; stopovers shown in yellow) maximize absolute greenness, whereas shrikes and nightingales track local peak greenness ($n$ = 18 and $n$ = 12, respectively; stopovers in red and blue). (Monthly comparisons are shown in fig. S2.)

individuals (fig. S4, A and B). The tracks of individual common cuckoos show an average greenness of 0.65 (corresponding to the 0.92 highest annual NDVI for any single grid cell or the 0.84 quantile compared to the highest possible value for random movement during consecutive biweekly periods) with a lowest average biweekly greenness of 0.51. Red-backed shrikes tracked an average greenness of 0.52 (0.80/0.70 quantiles) and thrush nightingales tracked an average greenness of 0.56 (0.84/0.75 quantiles). Only for cuckoos is the average greenness significantly higher than that expected from simulated random migration patterns, considering sub-Saharan migration distances covered from South Scandinavian breeding grounds ($P < 0.05$; Fig. 3C).

Moreover, red-backed shrikes and common nightingales closely tracked seasonal surplus in greenness ($P < 0.001$ for all species, sign test by biweekly period for local surplus greenness above average; Figs. 1, 2, and 3B and fig. S4). The average local surplus greenness along the migratory routes of individual shrikes is 1.21 (0.85 quantile for random movement) and that of nightingales is 1.19 (0.82 quantile), which is significantly higher ($P < 0.05$) than that of simulated random sub-Saharan tracks from Scandinavian breeding grounds for these species (Fig. 3D). Cuckoo tracks match local surplus greenness ($P < 0.001$, sign test) but not as closely, and their average local surplus greenness (1.15; 0.78 quantile) does not differ from that for simulated random tracks (Fig. 3D). The local surplus greenness quantiles were, on average, significantly higher for shrikes and nightingales ($P < 0.001$ and $P < 0.05$, respectively, paired $t$ test on each biweekly period) than greenness quantiles, whereas greenness quantiles were higher in cuckoos ($P < 0.01$). None of the species tracked here associated consistently with change in NDVI, neither with increasing nor decreasing vegetation greenness (Fig. 3E).

Comparisons of end-of-century projected changes in seasonal vegetation greenness and local surplus of greenness show some variation in how current migration patterns fit the projected conditions with regard to the exact timing of resource peaks (Fig. 4). If the migration pattern of tracked cuckoos is maintained, cuckoos would, in general, experience less greenness during fall and more greenness during winter and spring, but simulated tracks indicate that with slightly changed schedules, high greenness could still be achievable. The current schedules of shrikes and nightingales match the projected local surplus in resources less well during early fall and late spring migration but fit better during winter. Simulated tracks indicate that even with flexible schedules, the current match may be difficult to achieve (Fig. 4).

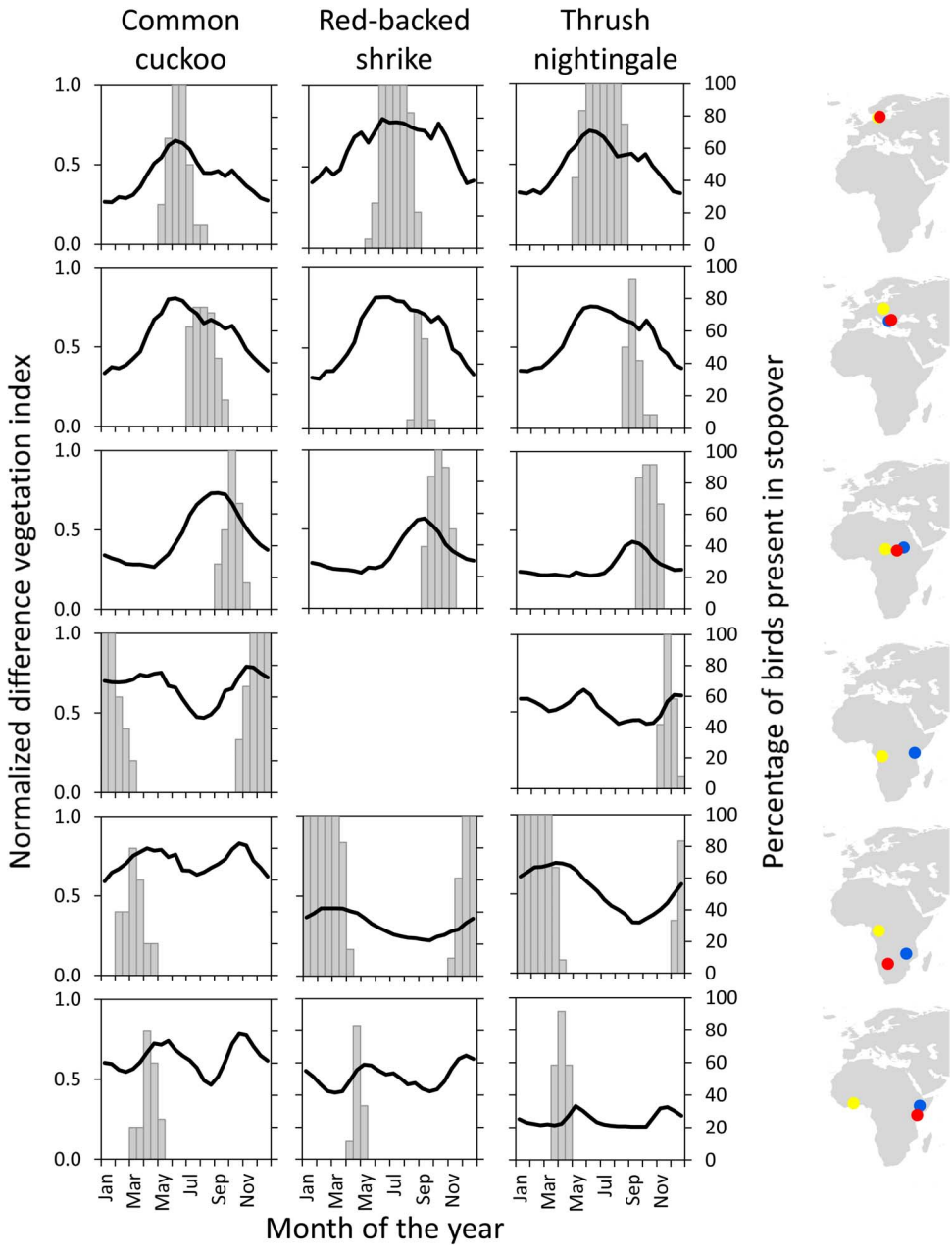


**Fig. 2. Timing of individual birds in relation to the seasonal development of NDVI in specific stopovers.** Each chart represents one of the major stopovers consistent among conspecific individuals. The black lines show the average NDVI over the course of a year on the average location of each stopover, and the bars show the percentage of conspecifics present in that stopover for at least 5 days in each biweekly period. Maps show the average location of the stopovers of cuckoos (yellow), red-backed shrikes (red), and thrush nightingales (blue).

## DISCUSSION

These three long-distance Palearctic-African migrants appear to track dynamics in seasonal resources within and across continents: Shrikes and nightingales dynamically track ephemeral surplus in local vegetation greenness, whereas cuckoos favor tracking regions with higher vegetation greenness throughout their annual cycle. Such strategies could occur in several of the longest-distance migrating species wintering south of the equator, for example, marsh warblers (*Acrocephalus palustris*) (*23*), but are potentially more constrained in species wintering further north in, for example, West Africa, where resources generally decline from early fall (*53*, *54*). The species we tracked showed no consistent pattern in timing, whether birds experienced increasing or decreasing greenness.

An inborn migration system is required to guide younger, inexperienced migrants (*55*). Potentially, the system could be relatively imprecise, causing large-scale stochastic juvenile site selection (*56*). Little is known about how flexible the program is and whether adult birds can switch sites according to local conditions (*57*). Recent evidence suggests that, at least in some cases, staging sites are still being used even when environmental conditions are poorer than anticipated for those sites (*44*).

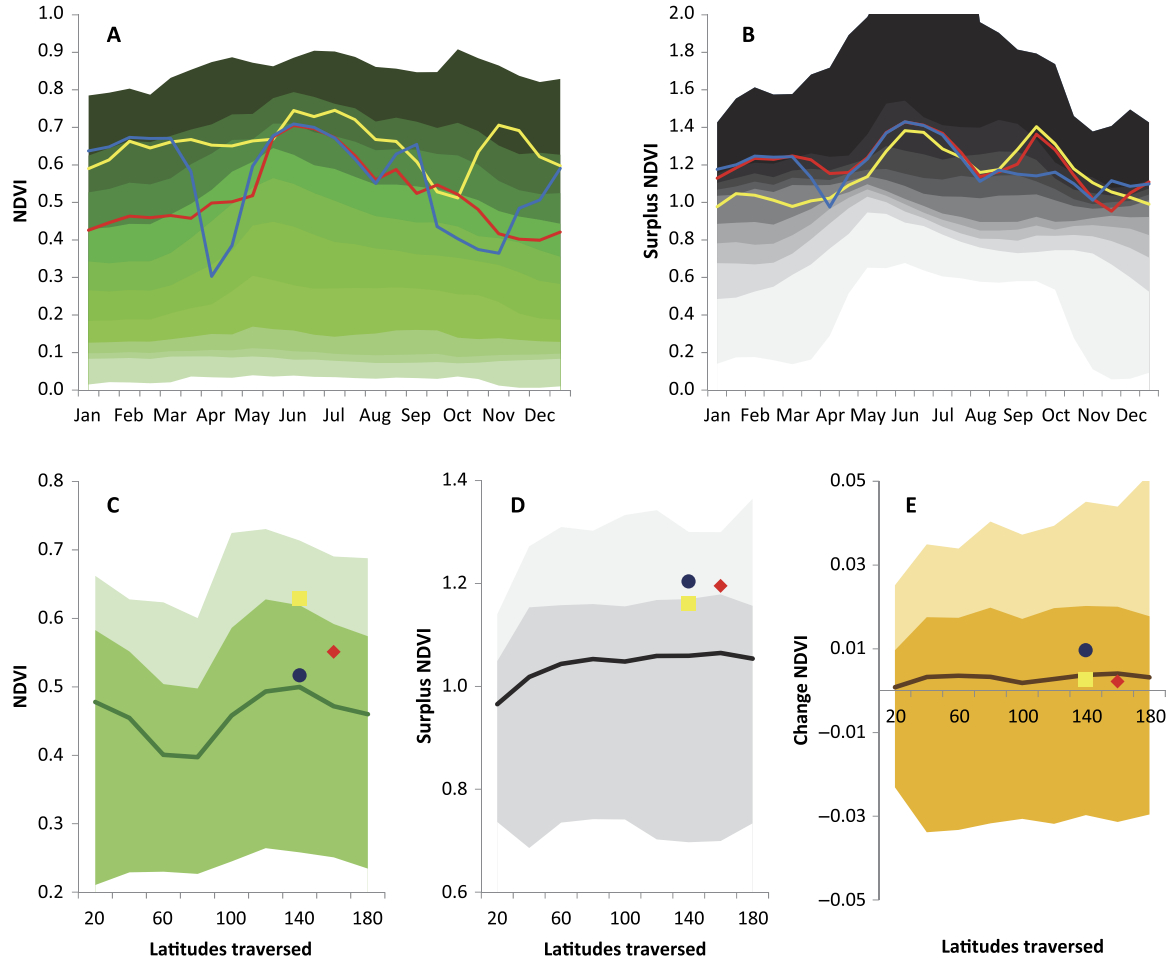


**Fig. 3. Greenness and surplus greenness along observed migratory tracks and comparisons with simulated tracks.** (**A**) Expected biweekly values of vegetation greenness and (**B**) surplus greenness of the locations used during the annual cycle by common cuckoos (yellow lines), red-backed shrikes (red lines), and thrush nightingales (blue lines). The background shows the biweekly NDVI and surplus NDVI quantiles for the Eurasian-African area considered. (**C** to **E**) Comparison of vegetation experienced along simulated tracks. The number of latitudes traversed reflects wintering latitude; traversing 180° corresponds to wintering in southern Africa. (C) Average greenness, NDVI [ranging from 0 (no greenness) to 1 (maximum greenness)], (D) surplus NDVI (surplus greenness; a value of 1 corresponds to average local NDVI; a value higher than 1 indicates vegetation greener than the average), and (E) change in NDVI (from the previous biweekly period), as a function of the latitudes traversed for simulated random migratory tracks from southern Scandinavian breeding grounds (55°N, 13°E) compared to observed tracks of cuckoos (yellow), shrikes (red), and nightingales (blue). Tracks were simulated as round trips (south and back) with a variable realistic number of migratory steps (two to eight) of variable length summing up to total latitudes traversed. Lines mark the average, dark shading denotes the lower 95% quantile, and pale shading indicates the upper 5% quantile from random simulations. Average NDVI and surplus NDVI were considered measures of average absolute and average surplus vegetation greenness, respectively.

Even though the birds tracked seasonal resources quite closely, there were still seasonal deviations. Part of this could be explained by the uncertainty in our tracking data or if no seasonal resources were available in some seasons. Furthermore, the considerable variation in breeding altitude for many species leads to considerable variation in timing of events even within species (*58*), and the importance of optimal timing of important life history events, such as breeding, could constrain timing of other events such as migration (*27*). Alternatively, a more consistent lack of fit for shorter periods may result because the current migration schedules arose during variable climate and seasonality in the past hundreds or even thousands of years and are not necessarily perfectly adapted to the climate during the past decade. This is supported by studies showing that migration routes are apparently relatively conserved (*59*, *60*).

The differences in vegetation tracking among the three species potentially result from differences in feeding biology. The cuckoos specialize on large insect larvae, whereas nightingales feed on smaller arthropods (and some fruit) and shrikes feed on adult insects (*61*). The larger larvae may be less common or less predictable in the more open areas occurring outside the Central African forests that are green year-round. Several other *Cuculus* species also spend the nonbreeding season in this area of high vegetation greenness but low seasonality, and the specialized food preference and parasitic lifestyle may favor leaving this area during breeding for suitable host species. However, ecological needs cannot easily explain why the sister species to the thrush nightingale, the common nightingale *Luscinia megarhynchos*, stay in West Africa for the winter (*62*). Jones (*36*) attributed such differences to some species' inability to tolerate aridity at the end of the dry season, indicating a physiological explanation. Alternatively, such differences could be caused by different population histories. However, trade-offs in costs of travel and availability of resources could also potentially lead to different stable strategies.

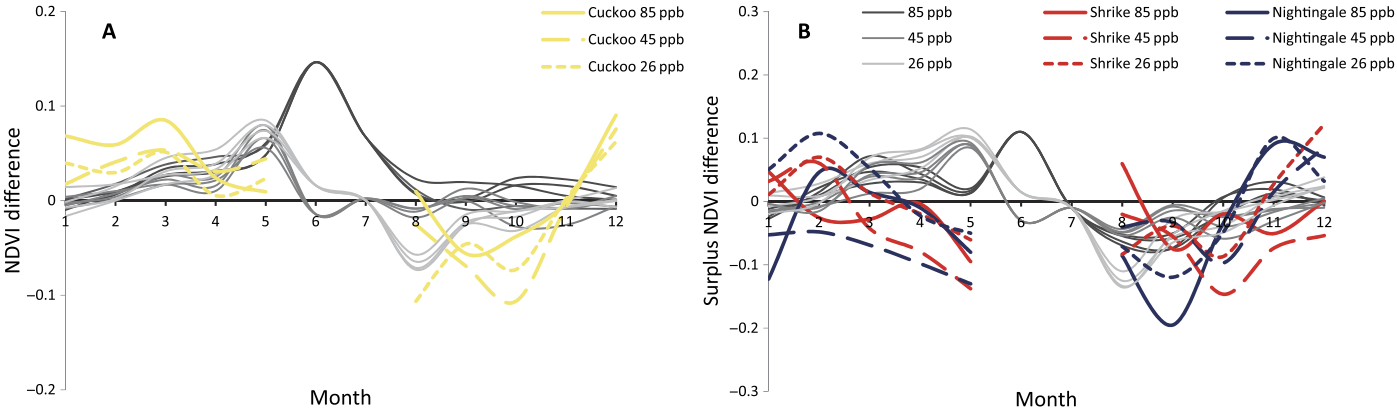


**Fig. 4. Potential effects of future climate change on matching of resources along migratory tracks.** Difference in projected (**A**) vegetation greenness, NDVI, and (**B**) vegetation surplus greenness, peak NDVI, along migratory tracks per month [1 (January) to 12 (December)] for 2011 and 2080 based on three climate change scenarios [26, 45, and 85 parts per billion (ppb) atmospheric $CO_2$]. We used biweekly projected data on precipitation and temperature to model NDVI. Simulated tracks traversed 100° to 160° of latitudes in total (starting at 55°N, 9°E), corresponding to a trans-Saharan migration (indicated by the four gray lines). The differences between the projected vegetation greenness for tracks in 2011 and 2080 of common cuckoos (yellow lines) and projected surplus vegetation greenness for shrikes (red lines) and nightingales (blue lines) are shown for comparison with the simulated random tracks. Positive values indicate expected improvement of environmental conditions (NDVI and peak NDVI) by 2080, and negative values indicate impoverished conditions or a mismatch. Breeding season data are omitted because of aberrant projections due to a low proportion of land cover.

Our climate projections of NDVI indicate poor matches between current schedules and future projected ones. However, given that the current match is attained under previous considerable spatial and temporal variation in climate within Africa (*53*), the match could indicate that migrants are well suited to adapt to changing seasonality (*63*). In light of the fast global climate and land use changes, it is essential to understand the migratory flexibility of long-distance migrants to ensure the successful long-term conservation management of such species (*64*). Future predictions of migratory patterns remain a significant challenge, considering the uncertainties in future climate change projections, how much local and regional climatic conditions are expected to change continental-wide distribution of resources, and how little we still know about the ability of individuals to adjust movement behavior to match these global changes.

## MATERIALS AND METHODS

### Experimental design

#### *Bird tracking data.*

Individual spatiotemporal location tracking of annual long-distance bird migration schedules from South Scandinavia (approximately 56°N, 12°E) to southern Africa and return was obtained using satellite-based radio tracking (common cuckoos, $n = 8$) (*46*) or light level–based geolocation (thrush nightingales, $n = 12$, and red-backed shrikes, $n = 18$) (*44*, *47*) in 2009–2014 (data available in data file S1). For satellite data, we excluded positions during 10-hour transmission periods indicating directed movement, and used the best positions for each transmission period (transmitter duty cycle, 10 hours on, 48 hours off) to indicate stopover locations during stationary periods, resulting in a total of 678 individual location estimates of cuckoos. We used archival light-level loggers (geolocators) to estimate the spatiotemporal locations of individual red-backed shrikes and thrush nightingales. The loggers store light levels, which can then be used to calculate the latitude and longitude from the time of sunrise and sunset converted to day length and local apparent noon and midnight. Latitude is inferred from the length of the solar day/night, and longitude is inferred from the time of local solar noon/midnight (*65*). To derive positional data from a light-level recording, the link between a certain light intensity value and the corresponding sun azimuth angle must be established. Here, we used a single fixed light-level threshold value of 2, corresponding to the sun well below the horizon, to define "sunrises" and "sunsets" (*66*). We then followed the Hill-Ekstrom calibration procedure (*67*, *68*) to determine the sun azimuth angle for red-backed shrikes and the breeding site calibration for thrush nightingales (*66*). The Hill-Ekstrom calibration procedure is based on an iterative process, where the most suitable corresponding sun azimuth value is established as the one minimizing the difference in latitude on either side of the equinox during periods when the birds were stationary, as indicated by longitude recordings. Because the stopover period of several nightingales did not extend to both sides of an equinox, we used breeding site calibration, that is, choosing the sun angle that produces the true latitude during the breeding season where the location was known. The data sets were initially adjusted for clock drift. The practical accuracy of the latitude and longitude obtained from similar geolocators has been reported to be 143 ± 62 km and 50 ± 34 km (±95% confidence interval), respectively (*69*). Given the lower precision of the geolocation data, we used estimated locations (mean position) for each stationary period, resulting in a total of 4279 stopover days with location estimates for nightingales and 7020 stopover days with location estimates for shrikes. We used the stationary periods when birds interrupted migration for more than 5 days, although birds could have moved short distances within a given area. The arrival and departure dates for the staging sites and wintering areas were determined from the two daily estimates for latitude and longitude data. Close to equinoxes, departure and arrival dates were estimated from longitude data only.

#### *Vegetation measures, NDVI, surplus NDVI, and change NDVI.*

The three species considered in this study are all insectivores. Overall, food availability could not be directly measured at the temporal and spatial scales in which our study was conducted. A familiar alternative is to use NPP as surrogate for local food availability (*70*). Here, we inferred NPP through NOAA-16 NDVI, AVHRR (Advanced Very High Resolution Radiometer) NDVI3g.v0 (*71*). The NDVI is the

difference (in reflectance) between the AVHRR near-infrared and visible bands divided by the sum of these two bands. It provides a measure of the degree of absorption by chlorophyll in red wavelengths and is proportional to canopy leaf chlorophyll density (*72*). The relationship between NDVI and rainfall is strongest in drier regions and might be influenced by other factors such as water and cloud cover (*73*). We used NDVI for biweekly (2-week) periods in each 2° latitude × 2° longitude cells across the whole annual migration routes (24 periods). To reflect the expected local vegetation greenness, we calculated for each cell an average of NDVI for each biweekly period during 2000–2010 (NDVI). The decadal data were chosen to match the climate experienced by birds before the trackings and, at the same time, to avoid the changes in climate that have occurred more recently. We chose to use decadal average biweekly values (expected values) as opposed to biweekly ones from the year the birds were tracked (experienced values) because migratory tracks are generally conserved between years and because stopovers most likely have evolved in response to expected values. Nevertheless, we also ran analyses directly based on the values from the year of tracking. In common cuckoos, the greenness of the NDVI from the year of tracking was higher than the decadal average NDVI ($P < 0.05$, pairwise $t$ test; fig. S4). For the other species, no differences were revealed between biweekly values from the year of tracking and average decadal biweekly values, and we report results for decadal averages (that is, expected values). To investigate the dependence of ephemeral local resources, we calculated for each cell the (surplus of) NDVI in each 2-week period compared to the annual average of local NDVI; this value was then averaged over the years 2000–2010, obtaining the surplus greenness (surplus NDVI; fig. S1). As with values of NDVI, we also used decadal average values of surplus NDVI. Values above 1 indicate values higher than the average for that cell, that is, a surplus. Change NDVI was calculated similarly for each cell as the average decadal increase in NDVI from the NDVI in the previous month. By focusing on food availability, we avoided modeling ecological regimes because it is unclear whether long-distance migrants generally track the same ecological regimes (the so-called "niche followers"), as suggested for several Nearctic-Neotropical migrant species (*34*), or change their ecological requirements during the annual cycle ("niche switchers"), as suggested for some *Dendroica* and *Spizella* species (*74*). For a few birds, we had repeated tracks. Five repeated tracks of red-backed shrikes revealed only smaller effects of individual consistency (fig. S4). Overall, the tracks showed high consistency at the spatial scale considered, and stopover locations were in general connected by direct flights. We explored the overall timing of individuals in each stopover relative to the expected timing of available resources by calculating the percentage of tracked birds present at a given stopover in every 2-week period and compare that to the decadal average value of NDVI at the average location of that stopover over the course of a year. The corrected vegetation data set used for estimating NDVI, surplus NDVI, and change NDVI was only available up until 2011. Thus, for the analyses of comparing stopover vegetation with average values, we used a full tracking data set with tracks up until 2014 and estimated vegetation data reported in 16-day periods (23 periods per year; available at http://modis.gsfc.nasa.gov/data/dataprod/mod13.php). Data are downloadable at a 0.05° latitude × 0.05° longitude resolution. Because of lower tracking data accuracy and for comparative reasons, we have resampled this to 2° latitude × 2° longitude cells. The general performance of the tracks was characterized as quantiles by comparing for each spatiotemporal location all possible values for land areas in Africa and the Palearctic region south of 58°N and west of 60°E to the observed value for the 2-week period where the birds were observed for greenness and surplus greenness, respectively. However, these will often involve unrealistic movements (without restrictions of travel speed).

## Statistical analysis

### *Simulation of migration.*

To test whether the observed tracks performed better than expected by chance, we compared observed tracks with simulated random tracks across the Palearctic region and Africa. Our aim was to capture overall resource optimization patterns. Given the infinite number of possible spatiotemporal schedules globally (*48*), we had to somewhat restrict the possibilities. Individual schedules were simulated as round trips, starting in the breeding area. Only southward steps were allowed during migration from the breeding grounds and only northward steps were allowed during return migration. Reverse movements as part of a general migration pattern are not suspected in any Palearctic songbird at the scale considered here (*75*), justifying this restriction. We ran individual-based simulations in R version 3.1.1 (*76*). Figure S3 illustrates the simulation procedure. Each individual started with a stationary 2-month period in the breeding area (56°N, 12°E; June to July). Tracks were then simulated as a full-year round trip (south and back) for a fixed number of latitudes traversed (20° to 180°) for the entire trip. The number of latitudes traversed corresponded to specific wintering latitudes so that a bird traversing 180° of latitude would migrate 90° south and would be wintering in southern Africa before migrating 90° of latitude north. Similarly, an individual traversing a total of 80° latitude would winter in the Sahara. For each individual simulated, a random number of migratory steps (two to eight), each occurring at a random time and with a random step length with the latter summing up to the fixed number of latitudes, for the entire trip were chosen. The most distant point ("wintering grounds") could be reached in any period of the year outside the stationary breeding season and for any of the migratory steps. There were no restrictions on the number of latitudes traversed per step. Simulations were run for every 20° of latitudes traversed from 20° to 180°. The number of tracks simulated for each number of latitudes depended on the quantity of interest. For current patterns focusing on annual greenness (Fig. 3), 2000 tracks were simulated for each latitude. For future simulations focusing on seasonal greenness (Fig. 4), 100 tracks were simulated for each latitude. We evaluated the different greenness measures (NDVI, surplus NDVI, and change NDVI from the previous 2-week period) of simulated tracks by comparing them with the values for observed tracks. To assess the degree to which greenness versus local surplus greenness predicts observed bird tracks, we compared the quantiles for each greenness measure in each of the 2-week intervals (24 periods per year) and used a simple sign test to indicate which model fitted the data best.

### *Projections of seasonal vegetation data.*

We explored the future performance of migration behavior based on climate forecast models. NDVI is known to be closely associated with aspects of climate that control plant growth, namely, temperature, solar radiation, and water availability (*77*, *78*). To project NDVI into the future, we constructed multiple regression models of NDVI with data from 2000 to 2010. Climate data at 1° resolution were obtained from the National Centers for Environmental Prediction "Final" Operational Global Analysis (http://rda.ucar.edu/datasets/ds083.2/) and are available from 1999 onward. Rainfall data were extracted from 3B42RT satellite data at a resolution of 0.25° and are available from

2000 onward (available at ftp://disc2.nascom.nasa.gov/data/TRMM/Gridded/Derived_Products/3B42RT/Daily/). NDVI models consisted of multiple linear regressions using biweekly measurements of NDVI, as response variables, and bi-weekly climate measurements, as predictor variables. We selected the mean, minimum, and maximum temperature, rainfall, relative humidity, and accumulated growing degree days [calculated following Wang *et al.* (*78*) and Yang *et al.* (*79*)] within every biweekly period over the period of comparison, that is, 2000–2010 for model fitting and 2035–2080 for model forecasts. The final choice of variables was made after examining pairwise relationships between NDVI and a suite of dynamic variables (wind speed and wind direction) and thermodynamic ones (the ones listed above). Because dynamic variables had weak and nonsignificant relationships with NDVI, they were discarded.

We forecasted end-of-century NDVI with climate data obtained for global climate models (*78*). The global climate change forecasts used considered the 26, 45, and 85 ppb $CO_2$ scenarios (low, medium, and high emissions, respectively) used in the latest Intergovernmental Panel on Climate Change V report (*80*, *81*). The relationship of NDVI with climate variables is known to be spatially nonstationary; that is, the magnitude and shape of the relationships among variables controlling it vary in space [for example, the work of Mora *et al.* (*82*)]. We were not aware of an appropriate mechanistic model capable of characterizing a lack of stationarity in NDVI-climate relationships. However, to quantify the potential errors arising from using a phenomenological linear model to estimate spatially nonstationary phenomena, we predicted NDVI into the same period for which historical, satellite-derived observations of NDVI exist and that coincided with the period used to fit forecast models. The adjustment between observed and predicted NDVI for this period was generally good and significant (fig. S5), thus supporting our choice of variables and models to forecast NDVI. It should be borne in mind that presented forecasts are conditional statements to examine "what if assumptions" of migratory patterns rather than full-fledged predictions of what the migratory patterns will be. The test data are not temporally independent from the training data (both from 2000 to 2010), thus causing model performance to be potentially inflated (*83*).

Matching of resources along migratory tracks was investigated as the difference in forecasted vegetation greenness, NDVI, local vegetation surplus greenness, and surplus NDVI between 2011 and 2080, based on three climate change scenarios (26, 45, and 85 ppb atmospheric $CO_2$). For simplicity, we focused our analyses on the end-of-century forecast only (figs. S6 and S7). We ran simulations with projected NDVI and surplus NDVI as we did for current data but starting at 55°N, 9°E rather than at 55°N, 13°E because of aberrant projections of the latter due to a low proportion of land cover. Breeding season tracking data have been omitted from future scenario analyses because all tracked breeding birds originated from the same few cells with aberrant projection.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/1/e1601360/DC1

fig. S1. Seasonal variation in NDVI across Africa and Europe.
fig. S2. Patterns of greenness and surplus greenness for each month.
fig. S3. Illustration of the random migratory track simulation procedure.
fig. S4. Individual variation in experienced and expected greenness and surplus greenness along migratory tracks.
fig. S5. Testing NDVI models.
fig. S6. Sequence of monthly differences between 2011 and 2080 of ΔNDVI and Δsurplus NDVI based on the (a) 26 ppb, (b) 45 ppb, and (c) 85 ppb projected climate change scenarios and stopover positions of common cuckoos, red-backed shrikes, and thrush nightingales.
fig. S7. Comparisons of current and modeled future NDVI and surplus NDVI for simulated tracks.
data file S1. Spatiotemporal positions of common cuckoos, red-backed shrikes, and thrush nightingales included in the study.

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Science Advances

# Resource tracking within and across continents in long-distance bird migrants

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